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OBSERVATIONS ON THE FORAGING PREFERENCES OF *LEIOPROCTUS* (*FILIGLOSSA*) RAYMENT (HYMENOPTERA: COLLETIDAE) IN EASTERN AUSTRALIA

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Abstract.—Fifty three bees representing three species in subgenus *Filiglossa* [(*Leioproctus davisi* Maynard (16 specimens), *L. filamentosa* (Rayment) Michener (36 specimens) and *L. hamatus* Maynard (one specimen)] were collected on nine *Persoonia* species (Proteaceae) distributed through New South Wales and Victoria. These records extend the foraging range of *L.* (*Filiglossa*) to ten *Persoonia* Sm. species; *P. arborea* F. Mueller, *P. asperula* L. Johnson & P. Weston, *P. champaepeuce* Lhotsky ex Meissner, *P. isophylla* K. Johnson & P. Weston, *P. lanceolata* Andrews, *P. mollis* subsp. *nectans* Krauss & L. Johnson, *P. pinifolia* L. Johnson & P. Weston, *P. silvatica* L. Johnson, *P. subvellutina* L. Johnson and *P. virgata* R. Br.. Female bees outnumbered males by 70%. Fifty five per cent of female bees and 43% of males carried significant loads of *Persoonia* pollen. One, female, *L. filamentosa* carried pollen from more than one *Persoonia* species when *Persoonia* species were sympatric and had overlapping flowering periods. Pollen analyses indicated that some females of *L. davisi* and males of *L. filamentosa* also foraged on coblooming Asteraceae and Myrtaceae. The poor collections of *L.* (*Filiglossa*) bees between 1946 and 1991 were possibly due to the failure to identify a single grain of *Persoonia* pollen carried by the holotype of *L. filamentosa.*

Key Words.—Insecta, *Leioproctus,* Colletidae, Australia

Until 1991 the *Leioproctus* (*Filiglossa*) *filamentosa* (Rayment) Michener (Colletidae) was known from only two specimens (Rayment 1959, Maynard 1994). One was collected in New South Wales by N. Rodd in 1947 and the second was collected in Queensland by J. Cardale in 1967. Neither collector appears to have kept field notes which flowers were visited by these bees.

Rayment (1959) erected the subgenus *Leioproctus* (*Filiglossa*) for three new species collected by Rodd (*filamentosa, striatula, proxima*). Rayment emphasized the excessive length of the mouthparts of these species suggesting "that the bees are associated with an equally remarkable flower." Michener (1965) moved both *striatula* and *promixma* to *Leioproctus* (*Euryglossidia*).

Rayment's prediction of a remarkable flower has never come true. All *Leioproctus* (*Filiglossa*) spp. have subsequently been collected on flowers of *Persoonia* Sm. since 1991 (Maynard 1994, Bernhardt & Weston in press). *Persoonia* remains one of the most common genera of shrubby Proteaceae in Australia consisting of approximately 90 species distributed through most coastal habitats (Weston 1991). The genus is treated as basal to the Proteaceae as *Persoonia* species lack such characters as proteioid root systems and floral protostigmas, considered apomorphic for most of the genera in the family (Johnson & Briggs 1975).

The extraordinary mouthparts of *L.* (*Filiglossa*) do not even appear to be evidence of a mutualistic coadaptation with *Persoonia* flowers as *L.* (*Filiglossa*) bees are not important pollinators of *Persoonia* species. To the contrary, the majority

of bees that pollinate *Persoonia* flowers belong to *Leioproctus* (*Cladocerapis*) species (Rayment 1950, Maynard 1992, Bernhardt and Weston in press).

Leioproctus (*Cladocerapis*) species appear to be facultative oligoleges on *Persoonia* flowers. The *Persoonia* pollen carried on their bodies is most likely to contact the stigma of the flower while the female bee rakes pollen from the anther slits or males and females probe the base of a flower for nectar. The *Persoonia* species native to eastern Australia produce radially symmetrical and tubular flowers. Each tepal is hinged at its base. When bees >6 mm long probe for nectar they depress one of the four tepals on each flower and insert their heads down the floral tube to collect nectar secreted by each of the four glands surrounding the stalked ovary (Rayment 1950, Bernhardt & Weston in press).

Bernhardt & Weston (in press) observed *L.* (*Filiglossa*) species collecting pollen from the anthers of *Persoonia* flowers but noted that these female bees rarely contacted the receptive stigma surrounded by the bases of the four anthers. *Leioproctus* (*Filiglossa*) species are less than 6 mm long and did not or could not depress the *Persoonia* tepals. These bees were observed inserting their elongated mouthparts between the seams of interlocking tepals at the apex of the floral tube. Walker (unpublished) observed similar feeding behaviour of *L. davisi* Maynard on *Persoonia arborea* F. Mueller.

Males of *L.* (*Filiglossa*) species observed on *P. silvatica* often avoided the tube's apex. They would insert their mouthparts at the base of the tube gaining direct access to the nectar chamber but avoiding the sexual organs of the flower. These observations suggest that the mouthparts of *L.* (*Filiglossa*) bees express a trend towards nectar robbing.

To help elucidate the zoogeography and foraging preferences of *L.* (*Filiglossa*) we present the following information. An updated list of *Persoonia* species on which *L.* (*Filiglossa*) species have been observed and captured; a cross-reference of bee species against the identifiable pollen they carried, and a re-examination of the literature to suggest why these insects may have been so under collected for over forty years.

Materials and Methods

Study Sites.—Gungulla Flat, SE of Waterfall, Royal National Park, New South Wales (NSW), 34°09′00″ S 151°00′30″ E alt. 150 m; dry sclerophyll forest; understory with *P. pinifolia* R. Br. (Plant Voucher, R. G. Coveny 15180) (Insect collections, 7 Feb 1991, 20 Feb 1992, 12 Mar 1992, 20 Mar 1992).

One km South of Pikes Saddle, NSW, 36°59′40″ S 149°34′00″ E, alt. 1280 m; dry sclerophyll woodland; understory with *P. silvatica* L. Johnson, *P. chamaepeuce* Lhotsky ex Meissner (Plant Voucher, P. H. Weston 1762), *P. asperula* L. Johnson & P. Weston (P. H. Weston 1763), (Insect collections, 19–20 Jan 1994).

Two km South of Pikes Saddle, NSW, 36°00′10″ S 149°34′00″ E, alt. 1280 m; dry sclerophyll forest; open understory with *P. silvatica* (Insect collection, 19–20 Jan 1994).

Approximately 0.3 km N of Banksia Street, on West Road Fire Trail, Hill Top, NSW, 34°20′30″ S 150°29′00″ E, alt. 560m; dry sclerophyll forest; shrubby understory with *P. mollis* subsp. *nectens* Krauss & L. Johnson (PHW 1775), *P. lanceolata* Andrews (Plant voucher, P. H. Weston 1776), (Insect collection, 2 Feb 1994, 19 Feb 1994).

Table 1. The collection record of *Leioproctus* (*Filiglossa*) species on *Persoonia* species in Queensland, New South Wales and Victoria since February 1991 (includes Maynard 1994).

Persoonia species	*Filiglossa* species			
	davisi	*filamentosa*	*hamatus*	*prolatus*
P. arborea	++	−	−	−
P. asperula	−	+	−	−
P. chamaepeuce	−	+	−	−
P. isophylla	−	+	−	−
P. lanceolata	−	+	−	−
P. mollis subsp. *nectens*	−	+	−	−
P. pinifolia	−	++	+	−
P. silvatica	−	+	−	−
P. subvellutina	−	+	−	−
*P. virgata**	−	+	−	+

++ = >10 specimens captured, + = 1–6 specimens captured, − = no specimens captured.

* The reference by Maynard (1994) recording *L. filamentosa* collected on *P. pinifolia* at Hastings Point on 7/ii/91 is corrected here. *Persoonia virgata* grows at the Hastings Point site not *P. pinifolia.*

Island Bend—Guthega road, 1.5 km WSW of Island Bend rest area, NSW, 36°20′00″ S 148°27′30″ E, alt. 1280 m; dry sclerophyll forest; shrubby, grass understory with *P. subvellutina* L. Johnson (Plant Voucher, P. H. Weston 1764) (Insect collection, 24 Feb 1994).

Greta Road, 1.0 km W of junction with Bumble Hill Road, Bumble Hill, NSW, 33°14′30″ S 151°14′45″ E, alt. 340 m; dry sclerophyll forest; shrubby understory with *P. isophylla* L. Johnson & P. Weston (Plant voucher, P. H. Weston 1781) (Insect collection, 15 Mar 1994).

About 9–15 km W of Mt. Baw Baw, Victoria, 37°50′ S 146′17″ E, alt. 930 m; wet sclerophyll forest; shrubby understory and subcanopy of *P. arborea* F. Muell. (Insect collection, K. Walker 7 Feb 1996).

Collection Methods and Pollen Analyses. Bees were netted and killed in jars with ethyl acetate fumes. Insect vouchers have been deposited in the Museum of Victoria, Melbourne. The single specimen of *L. hamatus* Maynard represents the holotype (Maynard 1994). Flowering plant vouchers were deposited in the Royal Botanic Garden, Sydney.

Methods for the removal and identification of pollen taxa from freshly killed bees follows Bernhardt & Walker (1984). As *L.* (*Filiglossa*) bees were killed in the same jar as other specimens of Hymenoptera that were taken while visiting *Persoonia* flowers the smaller bodies of the *L.* (*Filiglossa*) bees could have become contaminated with pollen dropped by the bodies of larger bees in the same jar. Therefore a pollen taxon was not recorded as present on the body of a bee unless >25 individual grains could be counted in each stained sample. Calberla's fluid was used to stain pollen and provide a semi-permanent mount (Ogden et. al. 1974).

Results and Discussion

The flowers of 20 *Persoonia* species were examined for the presence of *L.* (*Filiglossa*) species. Ten *Persoonia* species attracted four *L.* (*Filiglossa*) species (Table 1). *Persoonia pinifolia* and *P. virgata* R. Br. were the only shrubs studied

Table 2. Pollen load analyses of *Leioproctus* (subgenus *Filiglossa*) species collected on flowers of *Persoonia* species.

Taxon and gender	Pollen load			
	Persoonia only	*Persoonia* + other spp.	Other spp. only	No pollen
L. davisi				
female	1	0	5	5
male	0	0	0	5
L. hamatus				
female	1	0	0	0
L. filamentosa				
female	18	1	0	6
male	5	2	0	4
Totals	26	3	5	20
Grand Total = 54				

on which more than one *L.* (*Filiglossa*) species was captured. *Leioproctus filamentosa* (Rayment) visited the greatest number of *Persoonia* species and appears to have the widest distribution within the subgenus. *Leioproctus davisi* appeared to be restricted to subalpine, arborescent populations of *P. arborea* in Victoria and *L. hamatus* Maynard is still known from a single capture on *P. pinifolia* in New South Wales.

The captures of *L. filamentosa* on *Persoonia* species (Table 1) suggested that these bees may forage selectively on some *Persoonia* flowers. *Persoonia mollis* R. Br. is one of the most broadly distributed species in New South Wales (Weston 1991, Krauss & Johnson 1991). Bernhardt & Weston (in press) collected bees on five subspecies (*ledifolia* Cunn. ex Meissner) Kruss & Johnson, *leptophylla* Krauss & L. Johnson, *livens* Krauss & L. Johnson, *nectans, revoluta* Krauss & Johnson) of *P. mollis,* over three years at nine sites in New South Wales. Only a single specimen of *L. filamentosa* was collected on *P. mollis* subspecies *nectens* (Table 1).

Leioproctus filamentosa was collected on different *Persoonia* species in flower at the same site (e.g., on *P. asperula* and *P. chamaepeuce* at Pike's Saddle and on *P. lanceolata* and *P. mollis* subsp. *nectans* at the Hilltop site). Due to the difference in size and grain morphology of the pollens of *P. asperula* and *P. chamaepeuce,* it was possible to determine that one female of *L. filamentosa* had visited the flowers of *P. champaepeuce* before it was netted on *P. asperula.*

Leioproctus (*Filiglossa*) species were collected on *Persoonia* flowers from 0900 h until 1500 h with peaks in floral visitation from 1000 until 1300 h. The greatest number of bees were collected on *Peroonia* species in shady sites. The individual shrubs or small trees that seemed to be most likely to be visited by *L.* (*Filiglossa*) grew directly under the canopy (eg. *P. asperula, P. chamaepeuce, P. silvatica*) or stood in light gaps adjacent to dense, shadier sections of eucalypt woodland (eg. *P. lanceolata, P. pinifolia*).

Of the 53 specimens collected on *Persoonia* flower 54% carried significant loads (>25 grains/specimen) of *Peroonia* pollen (Table 2; Fig. 1). Over 16% also carried significant loads of pollen that did not belong to *Persoonia* flowers. These

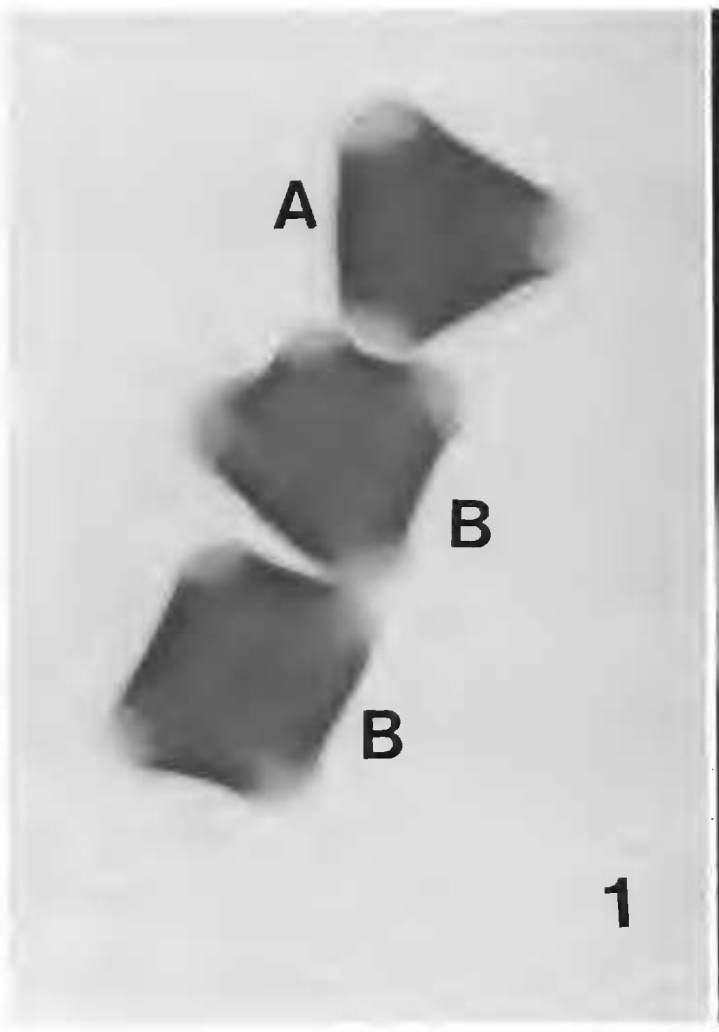

Figure 1. Hydrated pollen of *Persoonia chamaepeuce* carried by female *L. filamentosa* collected on *P. chamaepeuce*. A, regular, triporate grain; B, irregular, tetraporate grains (×511).

Figure 2. Head of female *L. filamentosa* collected on *P. silvatica* with pollen grains clinging to elongated palps (×40).

grains were identified most often on bees collected on *P. arborea* and *P. subvellutina* and belonged primarily to coblooming Asteraceae and Myrtaceae (Table 3). The presence of grains of Asteraceae on *L. davisi* suggest that the distribution of this species may be limited by topography and altitude and not by any specialization on *P. arborea* for pollen or nectar.

Females (55%) carried *Persoonia* pollen more often than males (43%; Table 2). Males of *L. filamentosa* were observed to either circle the shrubs in flower or

Table 3. Pollen load analyses of *L. davisi* and *L. filamentosa* carrying *Persoonia* pollen mixed with pollen of other species or no *Persoonia* pollen at all.

Bee taxon and gender	Pollen taxon				
	Ast	Myrt	*Persoonia*	Irid-Type	UD*
L. davisi					
female	5	0	0	0	0
L. filamentosa					
female	0	0	1	1	0
male	0	2	2	0	1

* Ast = Asteraceae (*Brachycome* and *Hypochaeris* types); Myrt = Myrtaceae (*Eucalyptus* type); Irid-Type (unidentified monocot, similar to Iridaceae); UD = unidentified dicot (tricolporate).

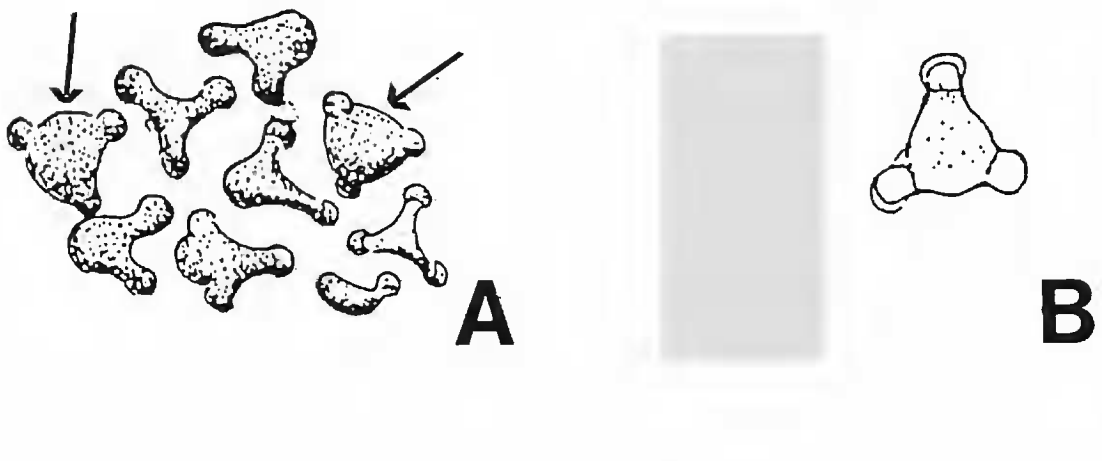

Figure 3. Illustrations of *Persoonia*-type pollen grains as drawn by T. Rayment. A = pollen grains from Rayment (1950) showing regular, hydrated grains (arrows) outnumbered by irregular and/or nonhydrated grains from flowers of *P. lanceolata*; B = pollen grain from Rayment (1959) showing an operculum over each pore. Rayment never included a scale in either publication and drawings here are reproduced twice the size of the originals.

hovered six to eight cm down wind of flowering branches. Males were not observed to forage actively for pollen, but they did contact dehiscent, anthers when perching on the flowers or while inserting their elongated mouthparts between the tepals at the apex of the floral tube. Pollen washes showed that only one male captured carried more than 90 grains of *Persoonia* pollen. In contrast, one female of *L. davisi,* one female of *L. hamatus* and fifteen females of *L. filamentosa* carried >100 grains of *Persoonia* each distributed in their scopae. *Persoonia* grains are often visible clinging to the elongated mouthparts of pinned specimens (Fig. 2).

Why has this bizarre colletid evaded entomologists for so many decades? One reason may be that Rayment (1959) was unable to identify the pollen grain found on the holotype of the male, *L.* (*Filiglosa*) *filamentosa.* In reviewing the original paper Rayment's drawing (Figure 3) shows a triangular-trilobate grain with three, large, operculate, pores produced by most of the Proteaceae in Australia (Johnson & Briggs 1975, Feuer 1986). Rayment's stippling of the grain suggests his microscope was sufficiently powerful to detect the scabrous ornamentations on the outer, pollen wall that are found throughout the genus, *Persoonia* (Feuer 1986).

Within the same paper, Rayment (1959) also suggested that large loads of pollen found on *L.* (*Euryglossidia*) *proxima* had also come from a member of the Myrtaceae (e.g., *Leptospermum*). Although the pollen of *Leptospermum* is triangular it lacks operculate pores and a scabrous pollen wall. Rayment's drawing of the pollen grain found on *L.* (*Euryglossidia*) *proxima* is almost identical to his drawing of the grain found on *L.* (*Filiglossa*) *filamentosa* (Fig. 3). If entomologists ever followed Rayment's suggestion and looked for *L. filamentosa* on myrtaceous flowers they would have attempted to collect this bee on blossoms it does not appear to visit with any great frequency (Table 3).

Rayment's difficulties with *Persoonia* pollen is most surprising considering his strong commitment to illustrating pollen grains found on bees and/or stored in their nests. A most self-consistent and dependable aspect of his fieldwork was that he identified the flower on which the bee was caught and then compared the pollen grains in the flower to grains removed from the bee's body and/or its pollen loaf (Rayment 1935). In fact, toward the end of his life Rayment completed a manuscript on the biology of the Australian heaths (Epacridaceae) containing

dozens of meticulous illustrations of pollen morphology, wall sculpture and germination (Rayment 1961). Genera within the Epacridaceae release their pollen grains in united packets of four known as tetrads. Rayment clearly discriminated between four, distinct modes of tetrad configuration.

In addition, Rayment (1950) also published a paper describing the pollination of *Persoonia mollis* by *Leioproctus* (*Cladocerapis*) species only nine years before his description of *Leioproctus* (*Filiglossa*) *filamentosa* (Rayment 1959). In this earlier paper Rayment emphasized the foraging behavior of *Leioproctus* (*Cladocerapis*) species on *Persoonia* flowers. As usual, he carefully drew *Persoonia* grains Norman Rodd provided from flowers of *Persoonia lanceolata*.

The drawing of *Persoonia* pollen in Rayment (1950) is based on a wet mount and shows that the author was familiar with the shape of hydrated, abortive and irregular-tetraporate grains (fig. 3). Compared to a modern photomicrograph (Fig. 1) all of Rayment's illustrations show the broad variation in the shape of *Persoonia* pollen.

In the case of *Leioproctus* (*Filiglossa*) species only two specimens, representing a single species, were collected for over forty years (Maynard 1994). Perhaps there is a lesson to be learned when sampling certain taxa that are obligate, floral foragers. When new species are caught in random sweeps, or lack fieldnotes as to foraging preferences, the success of future collections may be delayed. It may be easier to relocate these insects when distinctive pollens can be removed from the original specimens and identified using both standard palynological references and a back up collection of mounted grains or their photomicrographs.

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